Diminished large-scale functional brain networks in absolute pitch during the perception of naturalistic music and audiobooks

Brauchli, Christian ; Leipold, Simon ; Jäncke, Lutz

Abstract: Previous studies have reported the effects of absolute pitch (AP) and musical proficiency on the functioning of specific brain regions or distinct subnetworks, but they provided an incomplete account of effects of AP and musical proficiency on whole-brain networks. In this study, we used EEG to estimate source-space whole-brain functional connectivity in a large sample comprising AP musicians (n = 46), relative pitch (RP) musicians (n = 45), and Non-musicians (n = 34) during resting state, naturalistic music listening, and audiobook listening. First, we assessed the global network density of the participants' functional networks in these conditions. As revealed by cluster-based permutation testing, AP musicians showed a decreased mean degree compared to Non-musicians whereas RP musicians showed an intermediate mean degree not statistically different from Non-musicians or AP-musicians. This effect was present during naturalistic music and audiobook listening, but, crucially, not during resting state. Second, we identified subnetworks that drive group differences in global network density using the network-based statistic approach. We found that AP musicians showed decreased functional connectivity in major hubs of the default mode network during both music and audiobook listening compared to Non-musicians. Third, we assessed group differences in global network topology while controlling for network density. We did not find evidence for group differences in the clustering coefficient and characteristic path length. Taken together, we found first evidence of diminished whole-brain functional networks in AP musicians during the perception of naturalistic auditory stimuli. These differences might reflect a complex interplay between AP ability, musical proficiency, music processing, and auditory processing per se.

DOI: https://doi.org/10.1016/j.neuroimage.2019.116513

NeuroImage xxx (xxxx) xxx

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Diminished large-scale functional brain networks in absolute pitch during the perception of naturalistic music and audiobooks

Christian Brauchli [a,1,*], Simon Leipold [a,1], Lutz Jäncke [a,b,c,**]

[a] Division Neuropsychology, Department of Psychology, University of Zurich, Zurich, Switzerland
[b] University Research Priority Program (URPP) "Dynamics of Healthy Aging", University of Zurich, Zurich, Switzerland
[c] Department of Special Education, King Abdulaziz University, Jeddah, Saudi Arabia

ARTICLE INFO

Keywords:
Functional connectivity
Graph theory
EEG
Auditory

ABSTRACT

Previous studies have reported the effects of absolute pitch (AP) and musical proficiency on the functioning of specific brain regions or distinct subnetworks, but they provided an incomplete account of the effects of AP and musical proficiency on whole-brain networks. In this study, we used EEG to estimate source-space whole-brain functional connectivity in a large sample comprising AP musicians (n = 46), relative pitch (RP) musicians (n = 45), and Non-musicians (n = 34) during resting state, naturalistic music listening, and audiobook listening. First, we assessed the global network density of the participants' functional networks in these conditions. As revealed by cluster-based permutation testing, AP musicians showed a decreased *mean degree* compared to Non-musicians whereas RP musicians showed an intermediate mean degree not statistically different from Non-musicians or AP-musicians. This effect was present during naturalistic music and audiobook listening, but, crucially, not during resting state. Second, we identified the subnetworks that drove group differences in global network density using the network-based statistic approach. We found that AP musicians showed decreased functional connectivity between major hubs of the default mode network during both music and audiobook listening compared to Non-musicians. Third, we assessed group differences in global network topology while controlling for network density. We did not find evidence for group differences in the *clustering coefficient* and *characteristic path length*. Taken together, we found first evidence of diminished whole-brain functional networks in AP musicians during the perception of naturalistic auditory stimuli. These differences might reflect a complex interplay between AP ability, musical proficiency, music processing, and auditory processing per se.

1. Introduction

The previous decades of neuroscience have been remarkably influenced by the realization that "the brain is more than an assemblage of autonomous modules […]" (Sacks, 2010, p. 53). While distinct brain regions show some degree of functional specialization and might be sufficient to control basic functions necessary for survival (e.g., heart rate, breathing), it is striking how higher cognitive functions such as memory, attention, and intelligence result from interactions of multiple brain regions in large-scale networks (Bressler and Menon, 2010; Langer et al., 2012; Mesulam, 1990; Sporns et al., 2004). The human brain is nowadays conceived of as a complex network which is characterized by a robust and highly efficient information transfer between its constituent elements (Bullmore and Sporns, 2012, 2009; Park and Friston, 2013).

Given that a variety of cognitive functions are controlled by large-scale brain networks, the study of musicians with absolute pitch (AP) – the ability to identify a musical pitch without an external reference (Deutsch, 2013; Levitin and Rogers, 2005) – might be especially suited to study the neural underpinnings of the human brain network: During music production, musicians have to exert virtually every human cognitive function (Münte et al., 2002; Zatorre, 2005). This might cause increased functional connectivity within and between auditory and sensorimotor networks (Klein et al., 2016; Krishnan et al., 2018; Palomar-García et al., 2017; Zatorre et al., 2007). In addition, musicians with AP use cognitive functions and their underlying functional networks enabling them to effortlessly name and produce musical pitches.

* Corresponding author. University of Zurich, Department of Psychology Division Neuropsychology, Binzmühlestrasse 14, Box 25, Zurich, 8050, Switzerland.
** Corresponding author. University of Zurich, Department of Psychology, Division Neuropsychology, Binzmühlestrasse 14, Box 25, 8050, Zurich, Switzerland.
E-mail addresses: christian.brauchli@uzh.ch (C. Brauchli), lutz.jaencke@uzh.ch (L. Jäncke).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.neuroimage.2019.116513
Received 19 April 2019; Received in revised form 16 December 2019; Accepted 31 December 2019
Available online xxxx

It has been suggested that refined pitch categorization is a key property of AP (Zatorre, 2003). This perceptual advantage presumably relies on functional and structural alterations in the auditory cortex of AP musicians (Brauchli et al., 2019; Keenan et al., 2001; Lüders et al., 2004; McKetton et al., 2019; Ohnishi et al., 2001; Schlaug et al., 1995; Schulze et al., 2009; Wengenroth et al., 2014). Consistent with this notion, some EEG/MEG studies investigating event-related potential/event-related field correlates of AP have found differences in the amplitude and sources of early components presumably evoked by auditory cortex activation (Burkhard et al., 2019; Hirata et al., 1999; Hirose et al., 2004; Wengenroth et al., 2014; Wu et al., 2008).

Equal or better performance of AP musicians compared to relative pitch (RP) musicians in tasks requiring auditory working memory is accompanied by less activation in inferior frontal, middle frontal, and parietal brain regions (Leipold et al., 2019a; Schulze et al., 2009). In a similar vein, several EEG studies on AP have found reduced amplitudes in later event-related potential components associated with cognitive processes (Bischoff Renninger et al., 2003; Crummer et al., 1994; Hantz et al., 1992; Itoh et al., 2005; Klein et al., 1984; Leipold et al., 2019c, 2019b; Wayman et al., 1992). This could indicate that AP musicians use less (or different) neural resources or that they use the same resources more efficiently (Leipold et al., 2019a). They might also use different strategies not present in RP musicians, such as associative memory mechanisms. These mechanisms could be sustained by the dorsolateral prefrontal cortex (Bermudez and Zatorre, 2005; Zatorre et al., 1998).

Building on these findings, an AP-specific functional network has been reported, characterized by increased connectivity in the vicinity of the auditory cortex (Jäncke et al., 2012; Kim and Knösche, 2017; Loui et al., 2012), but also by increased connectivity within parietal and frontal brain regions (Brauchli et al., 2019). Taken together, both musical proficiency and AP ability have observable effects on large-scale functional brain networks.

To date, most studies have reported musician-specific alterations regarding the function of distinct brain regions or functional subnetworks. To the best of our knowledge, only two studies have investigated the effects of AP and musical proficiency on whole-brain networks so far: Investigating structural covariance networks based on anatomical similarities, Jäncke et al. (2012) reported decreased whole-brain connectivity in AP musicians, compared to both RP musicians and Non-musicians. RP musicians and Non-musicians did not differ from each other. It follows that AP – but not musical proficiency – has diminishing effects on whole-brain functional connectivity. Given that structural covariance networks reflect interactions in functional networks (Evans, 2013), the findings by Jäncke et al. (2012) contrast with the results of Loui et al. (2012), the second study investigating whole-brain connectivity, which reported increased functional connectivity in AP musicians compared to RP musicians.

In this study, we aimed to resolve the contradictory accounts of Jäncke et al. (2012) and Loui et al. (2012) by reevaluating whole-brain functional connectivity in AP musicians, RP musicians, and Non-musicians. Similar to the previous studies, we used a graph-theoretical framework to characterize the effects of AP and musical proficiency on the whole-brain functional network. As it is an open question whether the effects of AP and musical proficiency are prevalent during resting state (Klein et al., 2016; Loui et al., 2012; Palomar-García et al., 2017), or if they are evident only during auditory perception (Krishnan et al., 2018), we studied resting state and two naturalistic listening conditions, namely music and audiobook listening. We used naturalistic auditory stimuli in an ecological setting without a specific task because it has been repeatedly shown that the human brain processes stimuli in ecological settings differently than in conventional controlled settings (Hasson et al., 2004; Silbert et al., 2014). To further increase the ecological validity of our study, whole-brain functional networks were reconstructed from source-space EEG data, because this allows for a comfortable listening experience without interference by acoustic noise.

Our analyses were conducted in three steps: First, we assessed global network density during music listening, audiobook listening, and resting state by calculating the *mean degree* of the whole-brain network as a representative measure for the overall connectedness of the network. We extended the aforementioned studies by implementing cluster-based permutation testing (Drakesmith et al., 2015; Maris and Oostenveld, 2007; Nichols and Holmes, 2002). This technique which does not require the (arbitrary) choice of a specific threshold but uses a wide range of thresholds to evaluate group differences in network characteristics. For this first analysis, we used absolute thresholding based on functional connectivity values. Second, we analyzed which particular subnetworks might have driven global differences in functional connectivity between the groups. Third, we characterized group differences in global network topology during acoustic stimulation and resting state by calculating the *clustering coefficient* as a measure of network separation and *characteristic path length* as a measure of network integration. We again employed cluster-based permutation testing to avoid an arbitrary threshold choice. Here, we used proportional thresholding to assess the whole-brain network topology independent of the network density.

2. Methods

2.1. Participants

In recent years, studies in neuroscience have repeatedly been criticized for analyzing data from small samples (Button et al., 2013; Nord et al., 2017; Szucs and Ioannidis, 2017). Small samples not only reduce the probability of detecting an effect should a true effect exist, but also decrease the probability that a significant finding reflects a true effect (Button et al., 2013). Consequently, we analyzed a relatively large sample comprising 46 AP musicians, 45 RP musicians and 34 Non-musicians. All musicians were recruited from local conservatories and orchestras and were professionals, music students, or highly trained amateurs. Assignment to the groups of AP or RP musicians was based on self-report and could therefore not be attributed to an arbitrary cut-off in pitch-naming scores. Many of the musicians participated in other EEG and fMRI studies of our research group (Brauchli et al., 2019; Burkhard et al., 2019; Greber et al., 2018; Leipold et al., 2019a, 2019c, 2019b). In the current study, we excluded seven participants because of unsatisfactory data quality or missing EEG data. In addition to the data from musicians, we collected data from Non-musicians without musical training to further investigate effects of musical proficiency on whole-brain functional networks. The participants of the three groups were matched for age, sex, handedness, and cognitive capability (see Table 1).

The musician groups were also matched for musical training in terms of their age of commencement and the total of hours played during their lifetime (training effort). The musical aptitude of participants was quantified using the “Advanced Measures of Music Audiation” (AMMA) (Gordon, 1989). In this test, participants decided whether 30 successively presented pairs of short piano melodies were equivalent, different with respect to tonality, or different with respect to rhythmicity. Pitch-naming ability was evaluated using an online adaptation of an in-house test (Oechslin et al., 2010). Participants had to correctly name a total of 108 pure tones ranging from C3 to B5 (tuning: A4 = 440 Hz). Each tone was presented three times for 500 ms in a pseudo-randomized order, in which the same tone was never presented successively. Tones were preceded and followed by 2 s of Brownian noise. Pitch-naming scores were calculated as the percentage of correctly named tones without counting octave errors (Deutsch, 2013).

2.2. EEG recording, experimental procedure and data preprocessing

EEG data was continuously recorded using a 128-channel HydroCel Geodesic Sensor Net, a Net Amps 400 amplifier, and Net Station Acquisition software (Version 5.2.0.2) manufactured by Electrical Geodesic,

Table 1
Group demographics.

Measure	AP Musicians Mean (±SD)	RP Musicians Mean (±SD)	Non-Musicians Mean (±SD)	*P*-value[1]
Age (years)	26.09 (±4.87)	24.84 (±4.23)	24.29 (±3.42)	.15
Sex Ratio (female/all)	0.50 (–)	0.47 (–)	0.51 (–)	–
Handedness Ratio (right/[right + left + ambidextrous])	0.89 (–)	0.89 (–)	0.85 (–)	–
Cognitive Capability[a]	123.26 (±31.14)	134.63 (±26.89)	125.91 (±28.47)	.16
AoC[b] (years)	5.74 (±2.14)	6.40 (±2.47)	–	.18
Training Effort[c] (hours played)	16,952 (±12,626)	13,153 (±9,327)	–	.11
AMMA Total Score [d]	65.98 (±6.39)	62.69 (±6.90)	54.06 (±7.91)	<.001
Pitch-Naming Score (percent correct)	77.01 (±20.49)	22.08 (±18.18)	6.59 (±4.47)	<.001

[1] *P*-value based on one-way ANOVA or *t*-tests (as applicable).
[a] Kurztest für allgemeine Basisgrössen der Informationsverarbeitung (KAI) – total scores according to Lehrl et al. (1991).
[b] Age of commencement of musical training.
[c] Training effort measured as total of hours played during lifetime.
[d] "Advanced Measures of Music Audiation" (AMMA) according to Gordon (1989).

Inc. (EGI; Eugene, Oregon, USA). The data was collected at a sampling rate of 1,000 Hz with Cz as an online reference. Electrode impedance was kept below 25 kΩ by using a potassium-chloride solution. During EEG recording, participants sat comfortably in a chair in a dimly lit sound-shielded Faraday cage while they rested with their eyes open (EO), listened to excerpts from classical orchestral pieces, and to excerpts from audiobooks played on external speakers. The participants had no specific task but were instructed to fixate a white cross on a black background throughout EO resting-state measurement and acoustic stimulation. As it has been shown that concurrent tasks change both the listening experience and its EEG correlates (e.g., Jäncke et al., 2018), we explicitly did not use a particular task to keep the listening condition as natural as possible.

Our main objective was to identify the neural underpinnings of natural music listening in the three participant groups. The musical stimuli were previously used in other publications of our research group and are known to evoke the emotion fear (Gustav Holst: *Mars - The Bringer of War* from *The Planets*), sadness (Samuel Barber: *Adagio for Strings*), and joy (Ludwig van Beethoven: *Symphony No. 6*) (Baumgartner et al., 2006b, 2006a). The audiobook excerpts were taken as a control condition for the musical stimuli as we wanted to ensure that the effects of music listening were not due to emotional processing evoked by the music, but due to the acoustic stimulation in general. Thus, the audiobooks were chosen according to their potential to evoke the emotion fear (Steven King: *It*), sadness (Nicholas Sparks: *The Choice*), and joy (*Der kleine Nils*). The audiobook excerpts were presented in German in which all participants were fluent.

The auditory stimuli had a duration of 3 min each and were presented in a pseudo-randomized order after 3 min of EO resting-state measurement. The pseudo-randomization followed the rule that auditory stimuli of the same kind were always presented successively, i.e. in music or audiobook blocks. The order of blocks and the order of auditory stimuli within these blocks were randomized. Immediately after the presentation of an auditory stimulus, the participants were required to rate their perceived emotional valence and arousal using the self-assessment manikin (SAM; with nine levels: -4 – +4 [valence] and 0–8 [arousal]) (Bradley and Lang, 1994). Participants were also asked to identify the emotion inherent to the auditory stimulus in a single choice format with the options anger, joy, fear, disgust, and sadness. The whole procedure lasted for approximately 30 min.

The EEG data was preprocessed in BrainVision Analyzer (Version 2.0, Brain Products, Gilching, Germany). After the exclusion of twenty outer electrodes prone to muscle artifacts, a band-pass filter with a high-/low-pass criterion of 0.5/60 Hz (infinite impulse filter, Butterworth, 48 dB/oct) and a notch filter of 50 Hz were applied. Eye movement artifacts (blinks and saccades) were then removed using independent component analysis (Jung et al., 2000), and remaining bad electrodes were interpolated by spherical splines. Next, the data was re-referenced to the average of all remaining electrodes before EEG segments containing residual artifacts were automatically rejected. Based on the onset of EEG artifacts in single electrodes, adjacent EEG epochs (−200 ms to +200 ms) were rejected from all electrodes by applying the following criteria: a minimal/maximal allowed absolute amplitude difference of 0.5/120 μV within a time window of 200 ms and minimal/maximal amplitudes of −120/+120 μV. Based on the number of remaining (clean) EEG segments, data from auditory stimuli evoking joy (*Symphony No. 6* and *Der Kleine Nils*) was excluded from further analyses due to insufficient data quality during the presentation of the audiobook (which could have been caused by laughing and associated muscle artifacts). Lastly, the data was segmented according to the length of the stimuli and further split into epochs of 2 s. These epochs were exported for the graph-theoretical analysis of functional connectivity in the source space (see below).

2.3. Computation of functional connectivity in the source space

The sLORETA toolbox (V20160611) (http://www.uzh.ch/keyinst/loreta.htm) (Pascual-Marqui, 2002) was used for the computation of the whole-brain source-space functional connectivity (Lai et al., 2018; Schoffelen and Gross, 2009). Because both lower and higher EEG frequency bands have been related to auditory processing and memory functions (Bastiaansen et al., 2010; Edagawa and Kawasaki, 2017; Klimesch, 1997; Klimesch et al., 1994; Mai et al., 2016; Pesonen et al., 2006; Yordanova et al., 1998), functional connectivity was evaluated in three EEG frequency bands of interest: theta (4-7 Hz), alpha (8-12 Hz), and beta (13-30 Hz).

The whole-brain network comprised of 84 nodes used in previous publications of our research group (e.g., Klein et al., 2016). These nodes were defined using a single centroid voxel of each Brodmann area (BAs) as implemented in the sLORETA toolbox (42 BAs in each hemisphere). The functional connectivity between these nodes was quantified using *phase synchronization* which is defined as "the absolute value of the complex valued (hermitian) coherency between the normalized Fourier transforms" (Pascual-Marqui, 2007, p. 10), and takes a value between 0 (no synchronization) and 1 (perfect synchronization).

Please note that there exists currently no gold standard in the field concerning the use of a specific EEG source estimation algorithm, a particular functional connectivity measure, or a combination of these two elements. In contrast, a wide variety of EEG (and MEG) source estimation algorithms have been developed (Michel et al., 2004; e.g., Pascual-Marqui et al., 2009) and an even greater number of EEG/MEG functional connectivity measures (e.g., Schölvinck et al., 2013; Wendling et al., 2009). The here-employed (s)LORETA is a well-established algorithm that has been repeatedly validated (Grech et al., 2008; Grova et al., 2006; Wagner et al., 2003) and is also implemented in other popular EEG/MEG software packages apart from the sLORETA toolbox (Gramfort et al., 2014; Tadel et al., 2011). We used the connectivity measure of phase synchronization as it has been suggested that phase synchronization represents a fundamental mechanism for the integration of neuronal signals from distinct brain regions (Varela et al., 2001) and plays a major role in a diverse range of sensory and cognitive processes (Fell and Axmacher, 2011; Sauseng and Klimesch, 2008). Furthermore, the particular combination of (s)LORETA and phase synchronization has been successfully employed in a number of previous studies comparing functional connectivity between different groups (e.g., Mulert et al.,

2011; Ramyead et al., 2015).

Phase synchronization was computed separately for the EO resting state and each auditory stimulus based on the cross-spectra between EEG epochs before aggregating and averaging by block. As described above, auditory stimuli evoking joy were excluded. This resulted in 84 x 84 square connectivity matrices representing whole-brain networks, wherein a single cell contained the individual participants' phase synchronization in a given frequency band between two nodes during EO resting state, music listening, or audiobook listening. Exemplary difference connectivity matrices between Non-musicians, RP musicians, and AP musicians are shown in Fig. 1.

2.4. Graph-theoretical analysis of source-space connectivity

2.4.1. Global analysis of network density using absolute thresholding

We compared the density of the whole-brain networks of the three groups across different thresholds using the global graph-theoretical measure of *mean degree*. For this, the participants' connectivity matrices were analyzed using custom MATLAB code and functions of the Brain Connectivity Toolbox (V20170115) (http://www.brain-connectivity-toolbox.net) (Rubinov and Sporns, 2010). For each participant in each block and frequency band, the connectivity matrices were absolutely thresholded over a wide range of phase synchronization values from 0.1 to 0.9 in increments of 0.05. Subsequently, the mean degree of each thresholded matrix was computed as the average number of connections of every node to all connected other nodes in the network. This procedure yielded 17 mean degree values for each participant in each block and frequency, which was equivalent to the number of employed phase synchronization thresholds (0.1–0.9).

Group differences in mean degree across the 17 contiguous phase synchronization thresholds were examined separately per block (EO resting state, music block, audiobook block) and frequency band (theta, alpha, beta). Conventional parametric statistical tests are not well-suited to assess group differences in graph-theoretical measures across a high number of thresholds since the values across different thresholds are highly dependent (Jäncke et al., 2012; Langer et al., 2013). Group differences in graph-theoretical measures have hence been evaluated at a single threshold in previous studies (Loui et al., 2012). The choice of the threshold in such an analysis, however, is arbitrary and the analysis yields no information about the stability of the effect across multiple thresholds. Consequently, we used (nonparametric) cluster-based permutation testing, commonly employed for the evaluation of spatially or temporally dependent fMRI/EEG data (Maris and Oostenveld, 2007; Nichols and Holmes, 2002), to assess the statistical significance of group differences in mean degree and to correct for the family-wise error (FWE) that arises from multiple testing across different thresholds (Drakesmith et al., 2015; Langer et al., 2013).

In cluster-based permutation testing, the probability of *clustered* mean degree differences (i.e. differences across multiple contiguous phase synchronization thresholds) was estimated under the null distribution of no group differences. This null distribution was built by randomly permuting group labels and therefore removing group information. In detail, empirical mean degree differences at separate phase synchronization thresholds were first calculated using a one-way ANOVA with a single between-participant factor Group (AP musicians, RP musicians, Non-musicians) in R (V3.3.1; https://www.r-project.org/). Next, group labels were permuted in 5,000 iterations before calculating random group differences in mean degree for each permutation at each phase synchronization threshold using an identical ANOVA. Importantly, statistical dependency across contiguous phase synchronization thresholds was preserved in permutations; i.e. for a given permutation iteration, the random assignment of group labels was identical for all phase synchronization thresholds. Next, contiguous phase synchronization thresholds with *P*-values lower than 0.05 were combined to clusters. Note that in this case, the *P*-value is used as a descriptive cluster-defining threshold and not for inference. The cluster size in the empirical data served as the test statistic *k*. The null distribution of cluster sizes was estimated by storing the maximal cluster size of each permutation. Finally, the *P*-value of the empirical cluster was calculated as the proportion of cluster sizes under the null distribution that were larger than *k*. Because cluster-based permutation testing as employed here does not control the FWE-rate across frequency bands, the significance level was set to $\alpha = 0.05/3 = 0.017$.

Follow-up analyses were conducted to compare the mean degree of each pair of groups (AP vs. RP musicians, AP vs. Non-musicians, RP vs. Non-Musicians) in the blocks and frequency bands where statistically significant group differences in mean degree were identified. Here, we used an identical procedure as described above with the exception that the cluster-based permutation testing included a Welch test instead of a one-way ANOVA. As we conducted three post-hoc comparisons, we adjusted the significance level to $\alpha = 0.017$.

2.4.2. Local analysis of subnetworks driving network density

To better characterize which nodes and connections might have driven global group differences in network density, we identified group differences in subnetworks using the network-based statistic (NBS) approach (Zalesky et al., 2010) as implemented in the NBS toolbox (V1.2) (https://sites.google.com/site/bctnet/comparison/nbs). Analogously to cluster-based approaches, NBS estimates the probability of the size of a subnetwork showing group differences under the null distribution. Based on the results of the global analysis, we restricted the NBS analysis to the blocks and frequency bands where we found statistically significant group differences in mean degree. In detail, separately per block and frequency band, the connectivity matrices were compared between each pair of groups using a two-sample *t*-test at every connection. Next, connections where t-values exceeded 3.1 were combined to

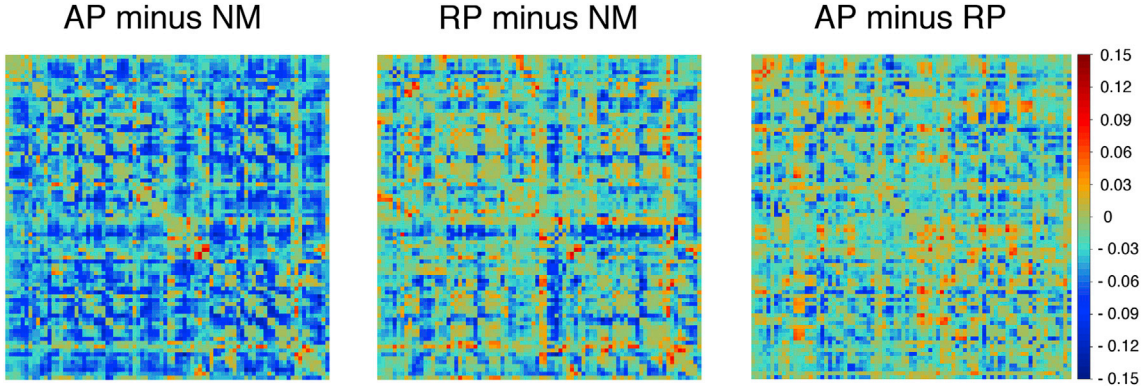

Fig. 1. Source-space functional connectivity between 84 regions of interest, derived from the beta frequency band during music listening. Difference connectivity matrices between AP musicians (AP), RP musicians (RP), and Non-musicians (NM) are shown.

form a subnetwork. Here, the t-value acted as a descriptive subnetwork-defining threshold. The size (extent) of the subnetwork served as the test statistic, which was compared to the null distribution of subnetwork sizes to obtain a *P*-value. This null distribution was built by repeating the procedure 5,000 times with randomly permuted group labels. As above, we used an adjusted significance level of $\alpha = 0.017$ for the number of pairwise comparisons. Statistically significant subnetworks were visualized using BrainNet Viewer (version 1.63) (https://www.nitrc.org/projects/bnv/) (Xia et al., 2013).

2.4.3. Global analysis of network topology using proportional thresholding

As the analysis of network density cannot give insights about the topology of the whole-brain networks, we also compared the groups regarding two graph-theoretical measures, *global clustering coefficient* and *characteristic path length*, which are informative regarding network topology. For this, we used proportional thresholding which equates the network density between participants. The clustering coefficient represents a graph-theoretical measure of separation within the network. It was based on *transitivity* and defined as the ratio of triangles to triplets. Characteristic path length represents a measure of network integration and was defined as the average shortest path length between all pairs of nodes in the network (Rubinov and Sporns, 2010).

All analysis steps for comparing the two measures between the groups were identical compared to the analysis of network density, except for the thresholding. Here, we thresholded the connectivity matrices based on the proportion of connections in the network that were retained after thresholding. We used a wide range of proportional thresholds from 5 to 90% retained connections in increments of 5%. As above, we adjusted the significance level to $\alpha = 0.017$ to correct for the number of investigated frequency bands.

3. Results

3.1. Pitch-naming ability and musical proficiency

A one-way ANOVA was conducted to examine the effect of Group (AP musicians, RP musicians, Non-musicians) on pitch-naming and AMMA total scores (see Fig. 2 for a visualization). As expected, the effect of Group on pitch-naming scores was highly significant ($F(2,122) = 205.71$, $P < 10^{-15}$, $\eta 2 = 0.77$). Post-hoc two-tailed Welch tests revealed that AP musicians demonstrated substantially higher pitch-naming scores than both RP musicians ($t(88.17) = 13.54$, $P < 10^{-15}$, $d = 2.83$) and Non-musicians ($t(50.70) = 22.59$, $P < 10^{-15}$, $d = 4.45$). Also, RP musicians demonstrated higher pitch-naming scores than Non-musicians ($t(50.90) = 5.50$, $P < 10^{-5}$, $d = 1.10$). This suggests that some RP musicians might have used RP-specific strategies (e.g., internal rehearsal of tones to calculate the musical interval) to achieve relatively high pitch-naming scores in comparison to untrained Non-musicians, as we have already suggested in previous publications of our research group (Brauchli et al., 2019; Leipold et al., 2019a).

Furthermore, the analyses revealed a significant effect of Group on AMMA total scores ($F(2,122) = 29.18$, $P < 10^{-10}$). As expected, Non-musicians performed significantly worse than AP musicians ($t(61.95) = -7.22$, $P < 10^{-9}$, $d = -1.69$) and RP musicians ($t(65.61) = -5.07$, $P < 10^{-5}$, $d = -1.17$). AP musicians had marginally higher AMMA total scores than RP musicians ($t(88.13) = 2.36$, $P = 0.021$, $d = 0.49$). This effect was driven by the better performance of AP musicians than RP musicians in tonal judgements ($t(87.02) = 2.69$, $P = 0.009$), but not in rhythmical judgements ($t(88.90) = 1.69$, $P = 0.095$). The enhanced performance of AP musicians in tonal judgements of the AMMA test might be explained by their exceptional pitch encoding abilities. The groups did not differ in their musical training in terms of age of commencement of musical training ($t(86.69) = 1.36$, $P = 0.177$) and training effort ($t(82.84) = 1.63$, $P = 0.106$). Since most of the Non-musicians did not report having received musical training in their lifetime, age of commencement and training effort were not statistically evaluated for Non-musicians. All Non-musicians with some sort of musical experience reported a training effort of less than 4,000 h over their lifetime.

3.2. Emotional judgements of music and audiobooks

The majority of the participants correctly identified the emotion fear after having listened to the fear evoking musical stimulus (52.46% correct) or audiobook (61.48% correct), as opposed to the guessing level of 20% (single choice format with five options, see above). In wrong emotion judgements, fear was mostly confused with the negative emotions anger (musical stimulus) or disgust (audiobook). Moreover, the participants were highly accurate in identifying the sadness evoking musical (88.52%) and audiobook stimulus (97.54%). In contradiction to their high accuracy in identifying negative emotions, many participants reported having experienced positive (valence rating > 0) emotions during music listening (fear: 64.75%, sadness: 34.43% of participants). This discrepancy between objectively recognized and subjectively experienced emotional valence was less evident for audiobooks (fear: 13.93%, sadness: 2.46% of participants with positive valence ratings).

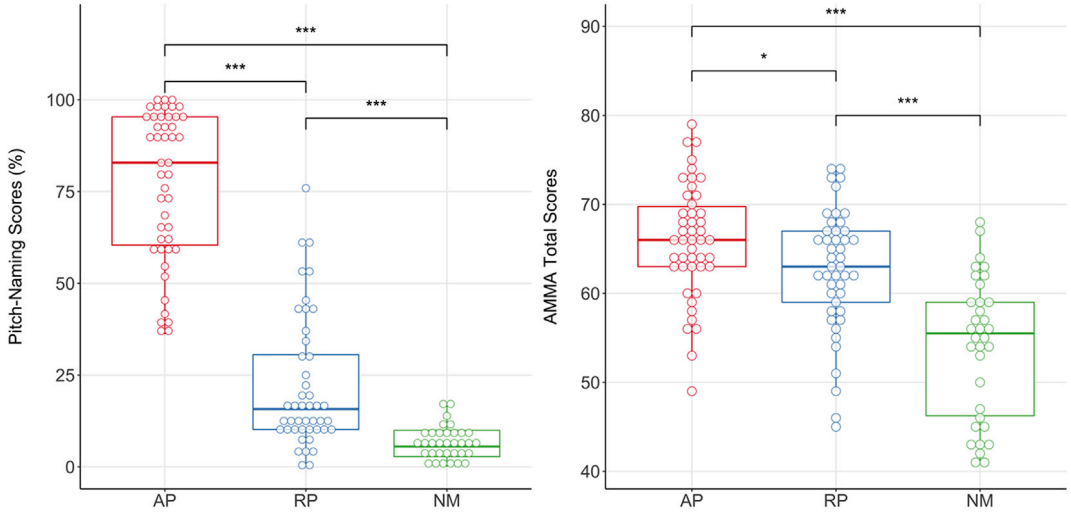

Fig. 2. Pitch-naming scores (left panel) and AMMA total scores (right panel) for AP musicians (AP), RP musicians (RP), and Non-musicians (NM). Asterisks denote statistically significant group differences (*p < 0.05, **p < 0.01, ***p < 0.001). AMMA = Advanced Measures of Music Audiation.

An ANOVA was conducted to examine the main effects of Group (AP musicians, RP musicians, Non-musicians) and Block (music, audiobook) and the interaction between Group and Block on arousal ratings. The analysis yielded a significant effect of Block ($F(1,119) = 151.51$, $P < 10^{-15}$) with higher arousal ratings for music (mean = 5.27 ± 1.94) than for audiobook blocks (mean = 3.20 ± 1.94). Moreover, the analysis yielded a significant interaction between Group and Block ($F(2,119) = 8.65$, $P < 0.001$). Post-hoc analyses revealed that this interaction effect was driven by lower music block arousal ratings of Non Musicians (mean = 4.42 ± 1.72) in comparison to both AP musicians (mean = 5.79 ± 1.76) ($t(68.98) = 3.99$, $P < 0.001$) and RP musicians (mean = 5.39 ± 2.07) ($t(73.79) = 2.59$, $P < 0.05$). Arousal ratings for audiobook blocks did not differ between groups. (Fig. 3).

3.3. Whole-brain network analyses

3.3.1. Global network density

Group differences in the mean degree of whole-brain functional networks during resting state, music listening, and audiobook listening were assessed using the cluster-based permutation testing procedure described above. The analysis yielded a statistically significant effect of Group (AP musicians, RP musicians, Non-musicians) on the mean degree derived from the beta frequency band exhibited during music listening ($P = 0.014$, FWE-corrected), with a cluster size k of 14 contiguous phase synchronization thresholds from 0.1 to 0.75. Follow-up analyses between each pair of groups revealed that this effect was driven by a lower mean degree of AP musicians compared to Non-musicians ($P = 0.016$, FWE-corrected, $k = 16$). We found no evidence for differences between RP and AP musicians or between RP and Non-musicians at any phase synchronization threshold ($k = 0$) (see Fig. 4).

For the audiobook listening, the analysis further revealed a significant effect of Group on the mean degree derived from the beta frequency band ($P = 0.04$, FWE-corrected, $k = 5$). Again, follow-up analyses revealed this effect to be driven by the lower mean degree of AP musicians compared to Non-musicians ($P < 0.001$, FWE-corrected, $k = 17$). We found no evidence for a group difference between RP and AP musicians or RP and Non-musicians at any threshold ($k = 0$). For the resting state block, there was no evidence for an effect of Group on the mean degree derived from the beta frequency band ($k = 0$). We also found no evidence for an effect of Group on the mean degree derived from the theta or alpha frequency band (see Supplementary Fig. 1).

We performed post-hoc two-tailed Pearson correlations to evaluate whether the mean degree of AP musicians, RP musicians, or Non-musicians during music listening was related to their pitch-naming ability, musical aptitude, or their music block arousal rating. We found no evidence for a correlation between the mean degree during music listening in the beta frequency band (averaged across thresholds from 0.1 to 0.75) and pitch-naming scores of AP musicians ($r = -0.18$, $P = 0.228$), RP musicians ($r = -0.12$, $P = 0.448$), or Non-musicians ($r = -0.14$, $P = 0.425$). Similarly, no evidence was found for a correlation between the mean degree and AMMA total scores of AP musicians ($r = 0.02$, $P = 0.908$), RP musicians ($r = 0.04$, $P = 0.799$), or Non-musicians ($r = -0.31$, $P = 0.075$). Finally, the analysis yielded no evidence for a correlation between the mean degree and music block arousal ratings of AP musicians ($r = -0.13$, $P = 0.384$), RP musicians ($r = -0.16$, $P = 0.285$), or Non-musicians ($r = -0.16$, $P = 0.369$).

3.3.2. Subnetworks driving differential network density

Based on the results of the network density analysis, we restricted the NBS analysis to the beta frequency band in the music and audiobook listening blocks. Fig. 5 visualizes the statistically significant subnetworks we identified in the pairwise group comparisons. For the music listening, we found a subnetwork of lower functional connectivity in AP musicians compared to Non-musicians ($P = 0.009$). Descriptively, the strongest group differences in functional connectivity were observed along the midline between the ventromedial prefrontal cortex including the anterior cingulate cortex (ACC) and the posterior cingulate cortex (PCC)/precuneus, and between the PCC/precuneus and middle temporal regions. Nodes with weaker connections included superior temporal, lateral frontal, and early visual regions (see Fig. 5, left panel). A strikingly similar network was identified in the comparison of AP musicians and Non-musicians for the audiobook listening ($P = 0.017$). Again, the descriptively strongest differences were found for connections between ventromedial prefrontal cortex and PCC/precuneus, and between PCC/precuneus and middle temporal regions.

A third subnetwork showed lower functional connectivity in RP musicians compared to Non-musicians during music listening, which was descriptively similar to the previously described networks (see Fig. 5, middle panel). However, this network was smaller in size and did not survive the adjustment of the significance level for multiple comparisons ($P = 0.019$). This corresponds well with the network density analysis, where we found descriptive, but not statistically significant differences between RP and Non-musicians. We did not identify differential subnetworks between AP and RP musicians during music and audiobook

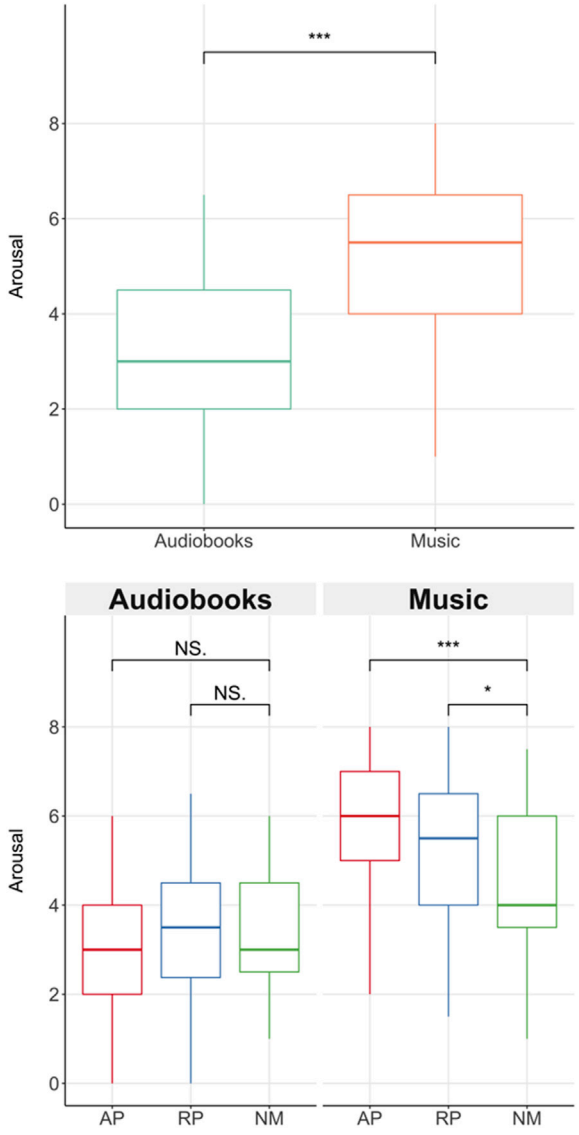

Fig. 3. Upper panel: Mean emotional arousal ratings for audiobooks and music, averaged over the three groups. Lower panels: Perceived emotional arousal in AP musicians (AP), RP musicians (RP), and Non-musicians (NM) when listening to audiobooks (left) or music (right). Asterisks denote statistically significant differences (*p < 0.05, **p < 0.01, ***p < 0.001).

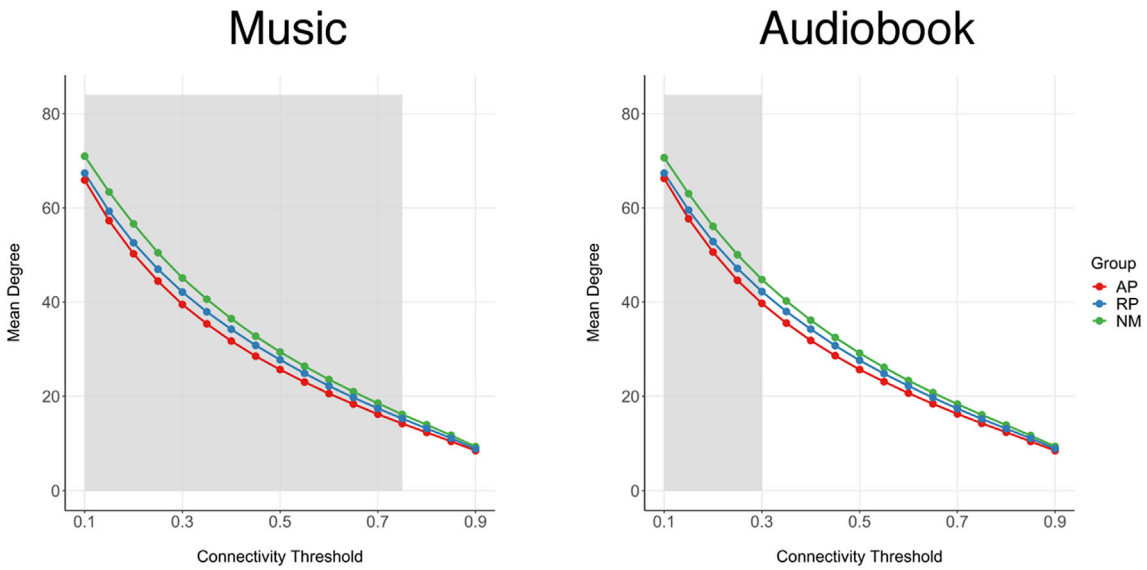

Fig. 4. The mean degree of AP musicians (AP), RP musicians (RP), and Non-musicians (NM) derived from the beta frequency band during music listening and during audiobook listening. For music listening (left panel), cluster-based permutation testing revealed a group effect across a broad range of connectivity thresholds (P = 0.014, FWE-corrected, gray-shaded area). This effect was driven by decreased mean degree of AP musicians compared to Non-musicians. For audiobook listening (right panel), the analysis revealed an equivalent group effect for a descriptively smaller range of connectivity thresholds (P = 0.04, FWE-corrected, gray-shaded area). Again, this effect was driven by a lower mean degree in AP compared to Non-musicians.

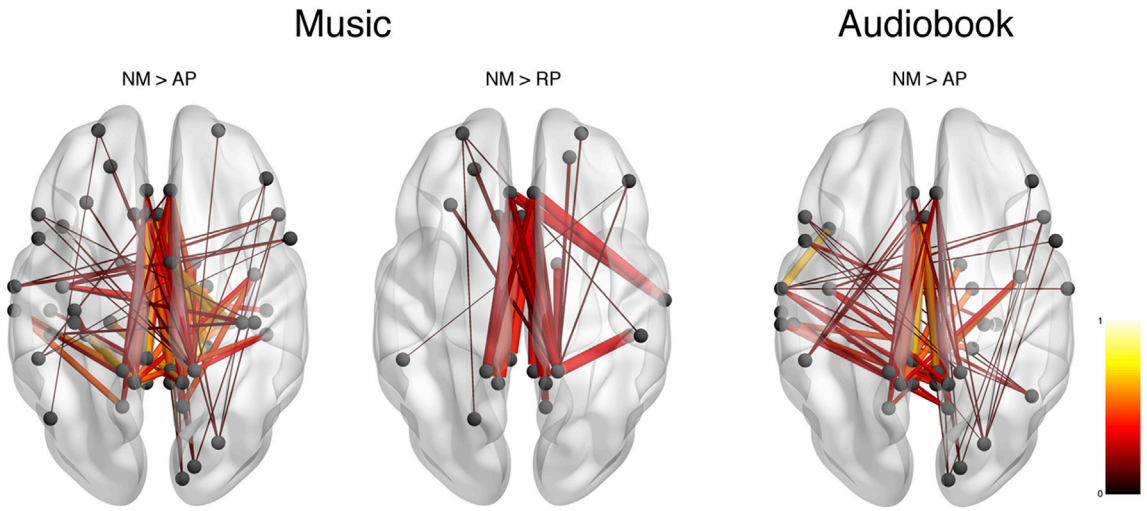

Fig. 5. Subnetworks identified by NBS showing group differences in functional connectivity derived from the beta frequency band during acoustic stimulation. Left panel: Increased functional connectivity in Non-musicians (NM) compared to AP-musicians (AP) during music listening (P = 0.009, FWE-corrected). Middle panel: Increased functional connectivity in Non-musicians compared to RP musicians (RP) during music listening (P = 0.019, FWE-corrected). This subnetwork did not survive the additional adjustment of the significance level for multiple pairwise group comparisons (α = 0.017). Right panel: Increased functional connectivity in Non-musicians compared to AP musicians during audiobook listening (P = 0.017, FWE-corrected). The color of the connections represents the absolute group difference in beta frequency band phase synchronization.

listening, and also not between RP and Non-musicians during audiobook listening.

3.3.3. *Global network topology*

Group differences in clustering coefficient and characteristic path length were evaluated using cluster-based permutation testing across a wide range of proportional thresholds. As shown in Fig. 6 (upper panels), we found no evidence for an effect of group on the clustering coefficient derived from the beta frequency band during music listening (P = 0.08, FWE-corrected, k = 3) or during audiobook listening (k = 0). We also detected no evidence for group differences in clustering coefficient during acoustic stimulation in the theta and alpha frequency bands (see Supplementary Fig. 2). For resting state, we found no evidence for group differences in all frequency bands.

Furthermore, as shown in Fig. 6 (lower panels), we found no evidence for an effect of group on characteristic path length in the beta frequency band during music or audiobook listening (both k = 0). We also found no evidence for group differences in characteristic path length in the theta or alpha frequency bands (see Supplementary Fig. 3). Again, we found no evidence for an effect of group on characteristic path length during resting state in all frequency bands. Please note that the significance level for all these analyses was adjusted to α = 0.017 to correct for the number

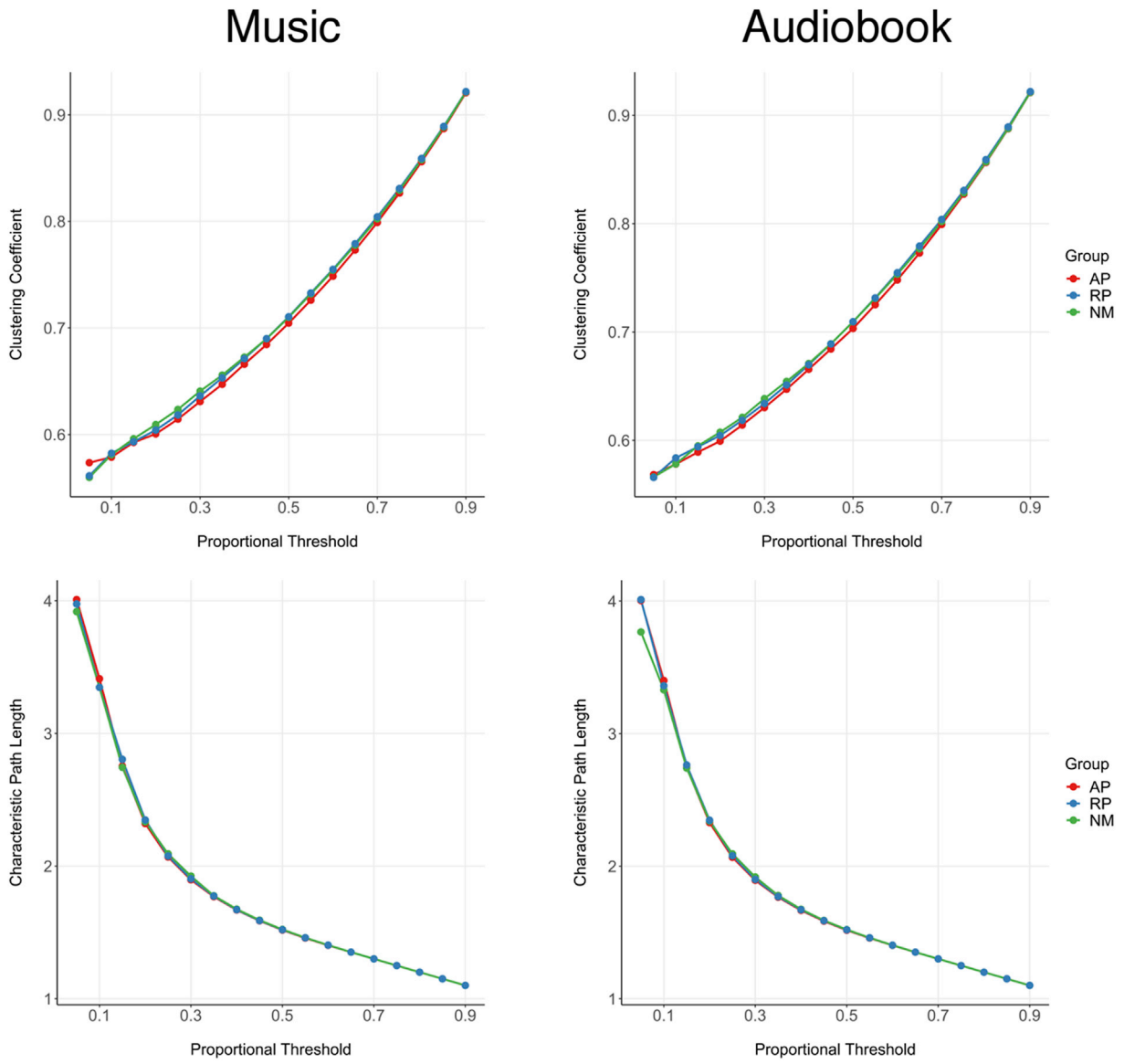

Fig. 6. Clustering coefficient and characteristic path length derived from the beta frequency band during music listening and during audiobook listening. We found no evidence for group differences between AP musicians (AP), RP musicians (RP), and Non-Musicians (NM) during music or audiobook listening. The proportional threshold values represent the proportion of the strongest connections that are preserved after thresholding.

of tested frequency bands.

4. Discussion

Previous studies have mainly explored the effects of AP and musical proficiency on the function of distinct brain regions or distinct functional subnetworks (Brauchli et al., 2019; Kim and Knösche, 2017; Klein et al., 2016; Loui et al., 2011; Luo et al., 2014, 2012; Palomar-García et al., 2017; Zamorano et al., 2017). These studies have provided incomplete insights into the effects of AP and musical proficiency on a global level of whole-brain networks. In addition, it is an open question if similar effects of AP and musical proficiency are observable during resting state and music listening (Klein et al., 2016; Krishnan et al., 2018; Loui et al., 2012). Using graph-theoretical analyses of network density and topology combined with cluster-based permutation testing, we assessed effects of AP and musical proficiency on whole-brain functional connectivity during resting state, music listening, and audiobook listening.

The analysis of network density revealed an effect of group on the mean degree of functional networks derived from the beta frequency band during both music and audiobook listening, but not during resting state. This effect was descriptively more extensive during music listening than during audiobook listening. Follow-up analyses showed that group differences in network density during auditory perception were driven by a decreased mean degree in AP musicians compared to Non-musicians, whereas for RP musicians, an intermediate mean degree not statistically different from Non-musicians or AP musicians was observed. The subsequent NBS analysis to identify subnetworks which could underlie the global differences in network density revealed the strongest group differences in functional connectivity between the ventromedial prefrontal cortex, the PCC/precuneus, and middle temporal brain regions. Consistent with the reduced mean degree, AP musicians showed lower functional connectivity between these brain regions than Non-musicians during music and audiobook listening. Finally, an analysis of network topology did not reveal evidence for group differences in clustering coefficient and characteristic path length during acoustic stimulation or resting state.

Taken together, for the first time, we find evidence for diminished whole-brain functional connectivity in AP musicians, consistent with

previously reported globally diminished structural covariance networks of AP musicians (Jäncke et al., 2012). Extending the findings of Jäncke et al. (2012), our results suggest that decreased whole-brain connectivity in AP musicians is not only a correlate of their AP ability. More likely, the diminishing effects were mediated through mechanisms related to AP ability, musical proficiency, music processing, and auditory processing per se.

One such mechanism might have operated through the interaction between AP ability and the special role of pitch in music. Pitch constitutes a primary perceptual dimension of music (Krumhansl, 2000; Plack et al., 2005) and varies far more subtly in music than in speech, where it is used for the purpose of intonation (Zatorre et al., 2002; Zatorre and Baum, 2012). Superior pitch chroma categorization in AP musicians might thus have the largest effect during music listening, which may explain the largest difference in network density during this condition.

The intermediate network density of RP musicians suggests an influence of musical proficiency and might relate to the musicians' benefits in auditory cognitive functions such as auditory memory (Pallesen et al., 2010; Zuk et al., 2014), auditory-motor integration (Baumann et al., 2007; Zatorre et al., 2007), and syntactic processing (Fitzroy and Sanders, 2013; Jentschke and Koelsch, 2009). Notably, these functions are relevant for both music and speech processing (Besson et al., 2011; Hickok et al., 2003; Patel, 2007, 2003), and they have been related to the beta frequency band (Bastiaansen et al., 2010; Edagawa and Kawasaki, 2017; Mai et al., 2016; Pesonen et al., 2006). Diminished beta coupling during music and audiobook listening but not during resting state might thus indicate a form of neural efficiency in musicians when such cognitive functions are stimulated (Leipold et al., 2019a). Although we did not find evidence for group differences in functional networks derived from the alpha and theta frequency bands, this does not mean that these EEG frequencies have no relevance for auditory sensory and cognitive functions. For example, oscillations in the alpha frequency band have been associated with music perception, imagery, and syntax (Ruiz et al., 2009; Schaefer et al., 2011), and the theta frequency band has previously been associated with auditory working memory (Albouy et al., 2017), and with AP and RP processing (Leipold et al., 2019b).

When considering the subnetworks underlying the globally diminished network density in AP musicians (see Fig. 5), it is noticeable that the major hubs lie medially in prefrontal and parietal regions, and in the medial temporal lobe. These brain regions have been considered as belonging to a large-scale brain network known as the default mode network (Greicius et al., 2003; Raichle, 2015; Raichle et al., 2001). The default mode network encompasses a specific set of brain regions that decrease in activation during a variety of cognitively demanding tasks (Shulman et al., 1997). Functional connectivity between default mode regions is highest during resting state but it is also present in sensory conditions with low attentional demands (Greicius et al., 2003; Greicius and Menon, 2004), such as the music and audiobook listening conditions used in the current study. In fact, it has been shown that functional connectivity in the default mode network is highly similar during music listening and resting state (Kay et al., 2012). The default mode network is usually reconstructed based on functional imaging data but it is also detectable using EEG/MEG (Brookes et al., 2011; Jann et al., 2009).

The lower functional connectivity within the default mode network in AP compared to Non-musicians during acoustic stimulation could be related to a higher cognitive engagement of the AP musicians during the (passive) perception of the acoustic stimuli. This would be consistent with the enhanced auditory cognitive functioning in musicians discussed in the previous paragraphs. Furthermore, we found a very similar subnetwork showing lower functional connectivity in RP compared to Non-musicians during music listening. This again points towards combined influences of AP and musical proficiency (see Fig. 5, middle panel). However, group differences in this subnetwork were more subtle as they did not survive the adjustment of the significance level for multiple pairwise group comparisons.

Apart from (auditory) cognitive processing, it might be that emotional processes had an impact on the functional networks: Group differences in functional connectivity in the beta frequency band seemed remarkably well paralleled by the groups' emotional response to music, which was generally more intense compared to audiobooks. Higher emotional intensity might be attributed to the increased potential of music to evoke complex emotions, as it is shown by the discrepancy between recognized and subjectively experienced emotional valence. This phenomenon is best described by paradox and ergo complex emotions like a "beautiful sadness" or an "invigorating fear" and it might have affected the participants' functional connectivity during music listening. However, emotional processing is more strongly associated with lower frequencies of the human EEG, especially the alpha frequency band (Baumgartner et al., 2006a; Harmon-Jones et al., 2010), in which no group differences in functional connectivity were found. Moreover, group differences were also present during audiobook listening for which participants reported a comparable degree of emotional arousal. We therefore propose the previously discussed cognitive processes during auditory perception as the most likely correlate of the AP musicians' decreased whole-brain connectivity although influences of emotion are also conceivable. The lack of evidence for correlations between the AP musicians' functional connectivity and their pitch-naming ability as well as their musical aptitude indicates a complex brain-cognition relationship rather than a single driving mechanism.

The results of this study stand in contrast to a previous report of *enhanced* whole-brain functional connectivity in AP musicians by Loui et al. (2012). The authors found both increased network density (as quantified by degree and connection strength) and network topology (as quantified by clustering coefficient and local efficiency). This divergence might be caused by methodological differences between the studies. First, in the previous study, correlation matrices were averaged across participants to obtain a mean functional network for AP musicians and RP musicians. Whole-brain functional connectivity group differences were then assessed in a statistical model with the AP and RP networks' individual nodes as observations. Such an approach defines its statistical power through network size (number of nodes) rather than by sample size (number of participants). Because it does not consider between-participant variance, it is not suited for statistical inference beyond the studied sample. In this study, we analyzed group differences based on the individual participants' whole-brain connectivity matrices using the individual participants as observations. Our approach allows for inference about the underlying populations from which our participants were drawn (Penny and Holmes, 2003). Second, the measures of network topology (clustering coefficient and local efficiency) assessed in the previous study were analyzed based on connectivity matrices that were absolutely thresholded (using a single connectivity value). As network density influences the measures of network topology used in the previous study, this approach does not allow for a differentiation between density and topology (Van Wijk et al., 2010). In this study, we separately analyzed network density using absolute thresholds and network topology using proportional thresholds (and thus controlling for network density) to disentangle these two aspects of the whole-brain functional network. However, the issue of absolute versus proportional thresholding in studies comparing groups is not yet resolved (Hallquist and Hillary, 2019; van den Heuvel et al., 2017).

Our findings should be interpreted within this study's limitations. First, because of the correlative nature of the study, we cannot determine if the observed group differences are consequences of AP and musical proficiency or causes that contribute to AP and musical proficiency. Especially regarding AP, there is an ongoing discussion about the origins of the phenomenon, which seem to be influenced by both genetic and environmental factors (Baharloo et al., 2000, 1998; Deutsch, 2002; Deutsch et al., 2009, 2006; 2004; Gregersen et al., 2013, 2001; 1999; Henthorn and Deutsch, 2007; Miyazaki et al., 2018; Profita and Bidder, 1988; Theusch et al., 2009; Theusch and Gitschier, 2011; Zatorre, 2003).

Second, we used EEG source estimation to reconstruct the whole-brain functional networks allowing us to study functional networks in

an ecologically valid setting. However, the source-space functional connectivity approach has an inherently limited spatial resolution, it can be affected by localization errors, and it depends strongly on the type and the particular parameters of the employed source estimation algorithm and the specific functional connectivity measure (Cho et al., 2015; Hincapié et al., 2017; Mahjoory et al., 2017; Schölvinck et al., 2013; Wendling et al., 2009). Specifically, we reconstructed source-space functional connectivity based on the established sLORETA source localization algorithm in combination with phase synchronization as a measure of functional connectivity. However, there are several other source estimation algorithms/functional connectivity measure-combinations. For example, previous studies have combined (and evaluated) beamforming with measures of amplitude envelope correlations, particularly on MEG data (Brookes et al., 2014; Colclough et al., 2016; O'Neill et al., 2017), whereas other studies used minimum norm estimation combined with phase synchronization measures (Hassan et al., 2014; Kabbara et al., 2017). As described above, a gold standard concerning these methods has yet to be established and the methods are still being evaluated.

Finally, source-based functional connectivity analyses suffer from the source leakage problem: Voxels located closely together in space can show spurious "connectivity" because of their non-independence. This in turn is caused by volume conduction (in EEG) and the coarse spatial resolution of the source estimation (Palva and Palva, 2012; Schoffelen and Gross, 2009). In this study, we tried to mitigate the effects of source leakage by using only the centroid voxel of each region of interest, which separates the individual regions in space. Furthermore, source leakage likely affects participants from all groups, so by contrasting the different groups, the leakage effects might cancel out to some extent. An additional action against source leakage, which we did not implement in this study, is the use of functional connectivity measures that exclude zero-lag interactions. However, it is not yet clear to what extent these interactions are artifactual or biological in nature, and even when using measures that exclude the zero-lag component, spurious interactions can still occur (Palva et al., 2018).

In conclusion, we found evidence for globally diminished functional networks in AP musicians during auditory perception and especially during music listening. The influence of cognitive and emotional mechanisms on the AP musicians' functional networks requires more careful examination in future studies specifically designed to investigate these mechanisms.

Author contributions section

CB collected data, designed and performed the analyses, and wrote the paper. SL contributed analysis tools, designed and performed the analyses, and wrote the paper. LJ conceived, designed, and supervised the study, and wrote the paper.

Declaration of competing interest

None.

Acknowledgements

We thank Alessandra E. Thomann for commenting and thus enhancing the quality of a previous version of the manuscript. We would also like to express our gratitude to Marc Zollinger, Yannic Dolder, Dawid Strzelczyk, Anna Speckert, Chantal Oderbolz, Fabian Demuth, Florence Bernays, Joëlle Albrecht, Kathrin Baur, Laura Keller, Melek Haçan, Nicole Hedinger, Pascal Misala, Petra Meier, Sarah Appenzeller, Tenzin Dotschung, Valerie Hungerbühler, Vanessa Vallesi, and Vivienne Kunz for their invaluable help in data acquisition and research administration. Furthermore, we thank Carina Klein for her assistance with the network analyses. Finally, we thank Marielle Greber and Anja Burkhard for their support within the larger absolute pitch project. This work was supported by the Swiss National Science Foundation (grant no. 320030_163149 to L.J.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2019.116513.

References

Albouy, P., Weiss, A., Baillet, S., Zatorre, R.J., 2017. Selective entrainment of theta oscillations in the dorsal stream causally enhances auditory working memory performance. Neuron 94, 193–206. https://doi.org/10.1016/J.NEURON.2017.03.015 e5.

Baharloo, S., Johnston, P.A., Service, S.K., Gitschier, J., Freimer, N.B., 1998. Absolute pitch: an approach for identification of genetic and nongenetic components. Am. J. Hum. Genet. 62, 224–231. https://doi.org/10.1086/301704.

Baharloo, S., Service, S.K., Risch, N., Gitschier, J., Freimer, N.B., 2000. Familial aggregation of absolute pitch. Am. J. Hum. Genet. 67, 755–758. https://doi.org/10.1086/303057.

Bastiaansen, M., Magyari, L., Hagoort, P., 2010. Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. J. Cogn. Neurosci. 22, 1333–1347. https://doi.org/10.1162/jocn.2009.21283.

Baumann, S., Koeneke, S., Schmidt, C.F., Meyer, M., Lutz, K., Jäncke, L., 2007. A network for audio–motor coordination in skilled pianists and non-musicians. Brain Res. 1161, 65–78. https://doi.org/10.1016/J.BRAINRES.2007.05.045.

Baumgartner, T., Esslen, M., Jäncke, L., 2006a. From emotion perception to emotion experience: emotions evoked by pictures and classical music. Int. J. Psychophysiol. 60, 34–43. https://doi.org/10.1016/j.ijpsycho.2005.04.007.

Baumgartner, T., Lutz, K., Schmidt, C.F., Jäncke, L., 2006b. The emotional power of music: how music enhances the feeling of affective pictures. Brain Res. 1075, 151–164. https://doi.org/10.1016/j.brainres.2005.12.065.

Bermudez, P., Zatorre, R.J., 2005. Conditional associative memory for musical stimuli in nonmusicians: implications for absolute pitch. J. Neurosci. 25, 7718–7723. https://doi.org/10.1523/jneurosci.1560-05.2005.

Besson, M., Chobert, J., Marie, C., 2011. Transfer of training between music and speech: common processing, attention, and memory. Front. Psychol. 2, 94. https://doi.org/10.3389/fpsyg.2011.00094.

Bischoff Renninger, L., Granot, R.I., Donchin, E., 2003. Absolute pitch and the P300 component of the event-related potential: an exploration of variables that may account for individual differences. Music Percept. Interdiscip. J. 20, 357–382. https://doi.org/10.1525/mp.2003.20.4.357.

Bradley, M.M., Lang, P.J., 1994. Measuring emotion: the self-assessment manikin and the semantic differential. J. Behav. Ther. Exp. Psychiatry 25, 49–59. https://doi.org/10.1016/0005-7916(94)90063-9.

Brauchli, C., Leipold, S., Jäncke, L., 2019. Univariate and multivariate analyses of functional networks in absolute pitch. Neuroimage 189, 241–247. https://doi.org/10.1016/J.NEUROIMAGE.2019.01.021.

Bressler, S.L., Menon, V., 2010. Large-scale brain networks in cognition: emerging methods and principles. Trends Cogn. Sci. 14, 277–290. https://doi.org/10.1016/J.TICS.2010.04.004.

Brookes, M.J., O'Neill, G.C., Hall, E.L., Woolrich, M.W., Baker, A., Palazzo Corner, S., Robson, S.E., Morris, P.G., Barnes, G.R., 2014. Measuring temporal, spectral and spatial changes in electrophysiological brain network connectivity. Neuroimage 91, 282–299. https://doi.org/10.1016/j.neuroimage.2013.12.066.

Brookes, M.J., Woolrich, M., Luckhoo, H., Price, D., Hale, J.R., Stephenson, M.C., Barnes, G.R., Smith, S.M., Morris, P.G., 2011. Investigating the electrophysiological basis of resting state networks using magnetoencephalography. Proc. Natl. Acad. Sci. U.S.A. 108, 16783–16788. https://doi.org/10.1073/pnas.1112685108.

Bullmore, E.T., Sporns, O., 2012. The economy of brain network organization. Nat. Rev. Neurosci. 13, 336–349. https://doi.org/10.1038/nrn3214.

Bullmore, E.T., Sporns, O., 2009. Complex brain networks: graph theoretical analysis of structural and functional systems. Nat. Rev. Neurosci. 10, 186–198. https://doi.org/10.1038/nrn2575.

Burkhard, A., Elmer, S., Jäncke, L., 2019. Early tone categorization in absolute pitch musicians is subserved by the right-sided perisylvian brain. Sci. Rep. 9, 1419. https://doi.org/10.1038/s41598-018-38273-0.

Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafò, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat. Rev. Neurosci. 14, 365–376. https://doi.org/10.1038/nrn3475.

Cho, J.H., Vorwerk, J., Wolters, C.H., Knösche, T.R., 2015. Influence of the head model on EEG and MEG source connectivity analyses. Neuroimage 110, 60–77. https://doi.org/10.1016/j.neuroimage.2015.01.043.

Colclough, G.L., Woolrich, M.W., Tewarie, P.K., Brookes, M.J., Quinn, A.J., Smith, S.M., 2016. How reliable are MEG resting-state connectivity metrics? Neuroimage 138, 284–293. https://doi.org/10.1016/j.neuroimage.2016.05.070.

Crummer, G.C., Walton, J.P., Wayman, J.W., Hantz, E.C., Frisina, R.D., 1994. Neural processing of musical timbre by musicians, nonmusicians, and musicians possessing absolute pitch. J. Acoust. Soc. Am. 95, 2720–2727. https://doi.org/10.1121/1.409840.

Deutsch, D., 2013. Absolute pitch. In: Psychol. Music. Elsevier, pp. 141–182. https://doi.org/10.1016/B978-0-12-381460-9.00005-5.

Deutsch, D., 2002. The puzzle of absolute pitch. Curr. Dir. Psychol. Sci. 11, 200–204. https://doi.org/10.1111/1467-8721.00200.

Deutsch, D., Dooley, K., Henthorn, T., Head, B., 2009. Absolute pitch among students in an American music conservatory: association with tone language fluency. J. Acoust. Soc. Am. 125, 2398–2403. https://doi.org/10.1121/1.3081389.

Deutsch, D., Henthorn, T., Dolson, M., 2004. Absolute pitch, speech, and tone language: some experiments and a proposed framework. Music Percept. 21, 339–356. https://doi.org/10.1525/mp.2004.21.3.339.

Deutsch, D., Henthorn, T., Marvin, E.W., Xu, H., 2006. Absolute pitch among American and Chinese conservatory students: prevalence differences, and evidence for a speech-related critical period. J. Acoust. Soc. Am. 119, 719–722. https://doi.org/10.1121/1.2151799.

Drakesmith, M., Caeyenberghs, K., Dutt, A., Lewis, G., David, A.S., Jones, D.K., 2015. Overcoming the effects of false positives and threshold bias in graph theoretical analyses of neuroimaging data. Neuroimage 118, 313–333. https://doi.org/10.1016/J.NEUROIMAGE.2015.05.011.

Edagawa, K., Kawasaki, M., 2017. Beta phase synchronization in the frontal-temporal-cerebellar network during auditory-to-motor rhythm learning. Sci. Rep. 7, 42721. https://doi.org/10.1038/srep42721.

Evans, A.C., 2013. Networks of anatomical covariance. Neuroimage 80, 489–504. https://doi.org/10.1016/J.NEUROIMAGE.2013.05.054.

Fell, J., Axmacher, N., 2011. The role of phase synchronization in memory processes. Nat. Rev. Neurosci. 12, 105–118. https://doi.org/10.1038/nrn2979.

Fitzroy, A.B., Sanders, L.D., 2013. Musical expertise modulates early processing of syntactic violations in language. Front. Psychol. 3, 603. https://doi.org/10.3389/fpsyg.2012.00603.

Gordon, E.E., 1989. Advanced Measures of Music Audiation. GIA Publications.

Gramfort, A., Luessi, M., Larson, E., Engemann, D.A., Strohmeier, D., Brodbeck, C., Parkkonen, L., Hämäläinen, M.S., 2014. MNE software for processing MEG and EEG data. Neuroimage 86, 446–460. https://doi.org/10.1016/J.NEUROIMAGE.2013.10.027.

Greber, M., Rogenmoser, L., Elmer, S., Jäncke, L., 2018. Electrophysiological correlates of absolute pitch in a passive auditory oddball paradigm: a direct replication attempt. eNeuro 5. https://doi.org/10.1523/ENEURO.0333-18.2018. ENEURO.0333-18.2018.

Grech, R., Cassar, T., Muscat, J., Camilleri, K.P., Fabri, S.G., Zervakis, M., Xanthopoulos, P., Sakkalis, V., Vanrumste, B., 2008. Review on solving the inverse problem in EEG source analysis. J. NeuroEng. Rehabil. 5, 25. https://doi.org/10.1186/1743-0003-5-25.

Gregersen, P.K., Kowalsky, E., Kohn, N., Marvin, E.W., 2001. Early childhood music education and predisposition to absolute pitch: teasing apart genes and environment. Am. J. Med. Genet. 98, 280–282. https://doi.org/10.1002/1096-8628(20010122)98:3<280::AID-AJMG1083>3.0.CO;2-6.

Gregersen, P.K., Kowalsky, E., Kohn, N., Marvin, E.W., 1999. Absolute pitch: prevalence, ethnic variation, and estimation of the genetic component. Am. J. Hum. Genet. 65, 911–913. https://doi.org/10.1086/302541.

Gregersen, P.K., Kowalsky, E., Lee, A., Baron-Cohen, S., Fisher, S.E., Asher, J.E., Ballard, D., Freudenberg, J., Li, W., 2013. Absolute pitch exhibits phenotypic and genetic overlap with synesthesia. Hum. Mol. Genet. 22, 2097–2104. https://doi.org/10.1093/hmg/ddt059.

Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc. Natl. Acad. Sci. U.S.A. 100, 253–258. https://doi.org/10.1073/pnas.0135058100.

Greicius, M.D., Menon, V., 2004. Default-mode activity during a passive sensory task: uncoupled from deactivation but impacting activation. J. Cogn. Neurosci. 1484–1492. https://doi.org/10.1162/0898929042568532.

Grova, C., Daunizeau, J., Lina, J.-M., Bénar, C.G., Benali, H., Gotman, J., 2006. Evaluation of EEG localization methods using realistic simulations of interictal spikes. Neuroimage 29, 734–753. https://doi.org/10.1016/J.NEUROIMAGE.2005.08.053.

Hallquist, M.N., Hillary, F.G., 2019. Graph theory approaches to functional network organization in brain disorders: a critique for a brave new small-world. Netw. Neurosci. 3, 1–26. https://doi.org/10.1162/netn_a_00054.

Hantz, E.C., Crummer, G.C., Wayman, J.W., Walton, J.P., Frisina, R.D., 1992. Effects of musical training and absolute pitch on the neural processing of melodic intervals: a P3 event-related potential study. Music Percept. 10, 25–42. https://doi.org/10.2307/40285536.

Harmon-Jones, E., Gable, P.A., Peterson, C.K., 2010. The role of asymmetric frontal cortical activity in emotion-related phenomena: a review and update. Biol. Psychol. 84, 451–462. https://doi.org/10.1016/J.BIOPSYCHO.2009.08.010.

Hassan, M., Dufor, O., Merlet, I., Berrou, C., Wendling, F., 2014. EEG source connectivity analysis: from dense array recordings to brain networks. PLoS One 9. https://doi.org/10.1371/journal.pone.0105041.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., Malach, R., 2004. Intersubject synchronization of cortical activity during natural vision. Science 303, 1634–1640. https://doi.org/10.1126/science.1089506.

Henthorn, T., Deutsch, D., 2007. Ethnicity versus early environment: comment on 'early childhood music education and predisposition to absolute pitch: teasing apart genes and environment' by Peter K. Gregersen, Elena Kowalsky, Nina Kohn, and Elizabeth west Marvin [2000]. Am. J. Med. Genet. 143A, 102–103. https://doi.org/10.1002/ajmg.a.31596.

Hickok, G., Buchsbaum, B., Humphries, C., Muftuler, T., 2003. Auditory–motor interaction revealed by fMRI: speech, music, and working memory in area Spt. J. Cogn. Neurosci. 15, 673–682. https://doi.org/10.1162/jocn.2003.15.5.673.

Hincapié, A.S., Kujala, J., Mattout, J., Pascarella, A., Daligault, S., Delpuech, C., Mery, D., Cosmelli, D., Jerbi, K., 2017. The impact of MEG source reconstruction method on source-space connectivity estimation: a comparison between minimum-norm solution and beamforming. Neuroimage 156, 29–42. https://doi.org/10.1016/j.neuroimage.2017.04.038.

Hirata, Y., Kuriki, S., Pantev, C., 1999. Musicians with absolute pitch show distinct neural activities in the auditory cortex. Neuroreport 10, 999–1002. https://doi.org/10.1097/00001756-199904060-00019.

Hirose, H., Kubota, M., Kimura, I., Yumoto, M., Sakakihara, Y., 2004. N100m in adults possessing absolute pitch. Neuroreport 15, 1383–1386. https://doi.org/10.1097/01.wnr.0000132921.90118.c4.

Itoh, K., Suwazono, S., Arao, H., Miyazaki, K., Nakada, T., 2005. Electrophysiological correlates of absolute pitch and relative pitch. Cerebr. Cortex 15, 760–769. https://doi.org/10.1093/cercor/bhh177.

Jäncke, L., Langer, N., Hänggi, J., 2012. Diminished whole-brain but enhanced peri-sylvian connectivity in absolute pitch musicians. J. Cogn. Neurosci. 24, 1447–1461. https://doi.org/10.1162/jocn_a_00227.

Jäncke, L., Leipold, S., Burkhard, A., 2018. The neural underpinnings of music listening under different attention conditions. Neuroreport 29, 594–604. https://doi.org/10.1097/WNR.0000000000001019.

Jann, K., Dierks, T., Boesch, C., Kottlow, M., Strik, W., Koenig, T., 2009. BOLD correlates of EEG alpha phase-locking and the fMRI default mode network. Neuroimage 45, 903–916. https://doi.org/10.1016/j.neuroimage.2009.01.001.

Jentschke, S., Koelsch, S., 2009. Musical training modulates the development of syntax processing in children. Neuroimage 47, 735–744. https://doi.org/10.1016/J.NEUROIMAGE.2009.04.090.

Jung, T.-P., Makeig, S., Humphries, C., Lee, T.-W., Mckeown, M.J., Iragui, V., Sejnowski, T.J., 2000. Removing electroencephalographic artifacts by blind source separation. Psychophysiology 37, 163–178. https://doi.org/10.1111/1469-8986.3720163.

Kabbara, A., El Falou, W., Khalil, M., Wendling, F., Hassan, M., 2017. The dynamic functional core network of the human brain at rest. Sci. Rep. 7, 2936. https://doi.org/10.1038/s41598-017-03420-6.

Kay, B.P., Meng, X., DiFrancesco, M.W., Holland, S.K., Szaflarski, J.P., 2012. Moderating effects of music on resting state networks. Brain Res. 1447, 53–64. https://doi.org/10.1016/j.brainres.2012.01.064.

Keenan, J.P., Thangaraj, V., Halpern, A.R., Schlaug, G., 2001. Absolute pitch and planum temporale. Neuroimage 14, 1402–1408. https://doi.org/10.1006/nimg.2001.0925.

Kim, S.-G., Knösche, T.R., 2017. Resting state functional connectivity of the ventral auditory pathway in musicians with absolute pitch. Hum. Brain Mapp. 38, 3899–3916. https://doi.org/10.1002/hbm.23637.

Klein, C., Liem, F., Hänggi, J., Elmer, S., Jäncke, L., 2016. The "silent" imprint of musical training. Hum. Brain Mapp. 37, 536–546. https://doi.org/10.1002/hbm.23045.

Klein, M., Coles, M.G.H., Donchin, E., 1984. People with absolute pitch process tones without producing a P300. Science 223, 1306–1309. https://doi.org/10.1126/science.223.4642.1306.

Klimesch, W., 1997. EEG-alpha rhythms and memory processes. Int. J. Psychophysiol. 26, 319–340. https://doi.org/10.1016/S0167-8760(97)00773-3.

Klimesch, W., Schimke, H., Schwaiger, J., 1994. Episodic and semantic memory: an analysis in the EEG theta and alpha band. Electroencephalogr. Clin. Neurophysiol. 91, 428–441. https://doi.org/10.1016/0013-4694(94)90164-3.

Krishnan, S., Lima, C.F., Evans, S., Chen, S., Guldner, S., Yeff, H., Manly, T., Scott, S.K., 2018. Beatboxers and guitarists engage sensorimotor regions selectively when listening to the instruments they can play. Cerebr. Cortex 28, 4063–4079. https://doi.org/10.1093/cercor/bhy208.

Krumhansl, C.L., 2000. Rhythm and pitch in music cognition. Psychol. Bull. 126, 159–179. https://doi.org/10.1037/0033-2909.126.1.159.

Lai, M., Demuru, M., Hillebrand, A., Fraschini, M., 2018. A comparison between scalp- and source-reconstructed EEG networks. Sci. Rep. 8, 12269. https://doi.org/10.1038/s41598-018-30869-w.

Langer, N., Pedroni, A., Gianotti, L.R.R., Hänggi, J., Knoch, D., Jäncke, L., 2012. Functional brain network efficiency predicts intelligence. Hum. Brain Mapp. 33, 1393–1406. https://doi.org/10.1002/hbm.21297.

Langer, N., Pedroni, A., Jäncke, L., 2013. The problem of thresholding in small-world network analysis. PLoS One 8, e53199. https://doi.org/10.1371/journal.pone.0053199.

Lehrl, S., Gallwitz, A., Blaha, L., Fischer, B., 1991. Theorie und Messung der geistigen Leistungsfähigkeit mit dem Kurztest KAI: Die allgemeinen Basisgrössen der Informationsverarbeitung. Vless Verlag.

Leipold, S., Brauchli, C., Greber, M., Jäncke, L., 2019a. Absolute and relative pitch processing in the human brain: neural and behavioral evidence. Brain Struct. Funct. 224, 1723–1738. https://doi.org/10.1007/s00429-019-01872-2.

Leipold, S., Greber, M., Sele, S., Jäncke, L., 2019b. Neural patterns reveal single-trial information on absolute pitch and relative pitch perception. Neuroimage 200, 132–141. https://doi.org/10.1016/J.NEUROIMAGE.2019.06.030.

Leipold, S., Oderbolz, C., Greber, M., Jäncke, L., 2019c. A reevaluation of the electrophysiological correlates of absolute pitch and relative pitch: No evidence for an absolute pitch-specific negativity. Int. J. Psychophysiol. 137, 21–31. https://doi.org/10.1016/j.ijpsycho.2018.12.016.

Levitin, D.J., Rogers, S.E., 2005. Absolute pitch: perception, coding, and controversies. Trends Cogn. Sci. 9, 26–33. https://doi.org/10.1016/j.tics.2004.11.007.

Loui, P., Li, H.C., Hohmann, A., Schlaug, G., 2011. Enhanced cortical connectivity in absolute pitch musicians: a model for local hyperconnectivity. J. Cogn. Neurosci. 23, 1015–1026. https://doi.org/10.1162/jocn.2010.21500.

Loui, P., Zamm, A., Schlaug, G., 2012. Enhanced functional networks in absolute pitch. Neuroimage 63, 632–640. https://doi.org/10.1016/j.neuroimage.2012.07.030.

Lüders, E., Gaser, C., Jäncke, L., Schlaug, G., 2004. A voxel-based approach to gray matter asymmetries. Neuroimage 22, 656–664. https://doi.org/10.1016/j.neuroimage.2004.01.032.

Luo, C., Guo, Z., Lai, Y., Liao, W., Liu, Q., Kendrick, K.M., Yao, D., Li, H., 2012. Musical training induces functional plasticity in perceptual and motor networks: insights from resting-state fMRI. PLoS One 7, e36568. https://doi.org/10.1371/journal.pone.0036568.

Luo, C., Tu, S., Peng, Y., Gao, S., Li, J., Dong, L., Li, G., Lai, Y., Li, H., Yao, D., 2014. Long-term effects of musical training and functional plasticity in salience system. Neural Plast. 2014 https://doi.org/10.1155/2014/180138.

Mahjoory, K., Nikulin, V.V., Botrel, L., Linkenkaer-Hansen, K., Fato, M.M., Haufe, S., 2017. Consistency of EEG source localization and connectivity estimates. Neuroimage 152, 590–601. https://doi.org/10.1016/j.neuroimage.2017.02.076.

Mai, G., Minett, J.W., Wang, W.S.-Y., 2016. Delta, theta, beta, and gamma brain oscillations index levels of auditory sentence processing. Neuroimage 133, 516–528. https://doi.org/10.1016/J.NEUROIMAGE.2016.02.064.

Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. J. Neurosci. Methods 164, 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024.

McKetton, L., DeSimone, K., Schneider, K.A., 2019. Larger auditory cortical area and broader frequency tuning underlie absolute pitch. J. Neurosci. https://doi.org/10.1523/JNEUROSCI.1532-18.2019, 1532–18.

Mesulam, M.-M., 1990. Large-scale neurocognitive networks and distributed processing for attention, language, and memory. Ann. Neurol. 28, 597–613. https://doi.org/10.1002/ana.410280502.

Michel, C.M., Murray, M.M., Lantz, G., Gonzalez, S., Spinelli, L., Grave de Peralta, R., 2004. EEG source imaging. Clin. Neurophysiol. 115, 2195–2222. https://doi.org/10.1016/J.CLINPH.2004.06.001.

Miyazaki, K., Rakowski, A., Makomaska, S., Jiang, C., Tsuzaki, M., Oxenham, A.J., Ellis, G., Lipscomb, S.D., 2018. Absolute pitch and relative pitch in music students in the east and the west. Music Percept. 36, 135–155. https://doi.org/10.1525/mp.2018.36.2.135.

Mulert, C., Kirsch, V., Pascual-Marqui, R., McCarley, R.W., Spencer, K.M., 2011. Long-range synchrony of gamma oscillations and auditory hallucination symptoms in schizophrenia. Int. J. Psychophysiol. 79, 55–63. https://doi.org/10.1016/J.IJPSYCHO.2010.08.004.

Münte, T.F., Altenmüller, E., Jäncke, L., 2002. The musician's brain as a model of neuroplasticity. Nat. Rev. Neurosci. 3, 473–478. https://doi.org/10.1038/nrn843.

Nichols, T.E., Holmes, A.P., 2002. Nonparametric permutation tests for functional neuroimaging: a primer with examples. Hum. Brain Mapp. 15, 1–25. https://doi.org/10.1002/hbm.1058.

Nord, C.L., Valton, V., Wood, J., Roiser, J.P., 2017. Power-up: a reanalysis of "power failure" in neuroscience using mixture modeling. J. Neurosci. 37, 8051–8061. https://doi.org/10.1523/JNEUROSCI.3592-16.2017.

O'Neill, G.C., Tewarie, P.K., Colclough, G.L., Gascoyne, L.E., Hunt, B.A.E., Morris, P.G., Woolrich, M.W., Brookes, M.J., 2017. Measurement of dynamic task related functional networks using MEG. Neuroimage 146, 667–678. https://doi.org/10.1016/j.neuroimage.2016.08.061.

Oechslin, M.S., Meyer, M., Jäncke, L., 2010. Absolute pitch — functional evidence of speech-relevant auditory acuity. Cerebr. Cortex 20, 447–455. https://doi.org/10.1093/cercor/bhp113.

Ohnishi, T., Matsuda, H., Asada, T., Aruga, M., Hirakata, M., Nishikawa, M., Katoh, A., Imabayashi, E., 2001. Functional anatomy of musical perception in musicians. Cerebr. Cortex 11, 754–760. https://doi.org/10.1093/cercor/11.8.754.

Pallesen, K.J., Brattico, E., Bailey, C.J., Korvenoja, A., Koivisto, J., Gjedde, A., Carlson, S., 2010. Cognitive control in auditory working memory is enhanced in musicians. PLoS One 5, e11120. https://doi.org/10.1371/journal.pone.0011120.

Palomar-García, M.Á., Zatorre, R.J., Ventura-Campos, N., Bueichekú, E., Ávila, C., 2017. Modulation of functional connectivity in auditory-motor networks in musicians compared with nonmusicians. Cerebr. Cortex 27, 2768–2778. https://doi.org/10.1093/cercor/bhw120.

Palva, J.M., Wang, S.H., Palva, S., Zhigalov, A., Monto, S., Brookes, M.J., Schoffelen, J.M., Jerbi, K., 2018. Ghost interactions in MEG/EEG source space: a note of caution on inter-areal coupling measures. Neuroimage 173, 632–643. https://doi.org/10.1016/j.neuroimage.2018.02.032.

Palva, S., Palva, J.M., 2012. Discovering oscillatory interaction networks with M/EEG: challenges and breakthroughs. Trends Cogn. Sci. https://doi.org/10.1016/j.tics.2012.02.004.

Park, H.-J., Friston, K., 2013. Structural and functional brain networks: from connections to cognition. Science 342, 1238411. https://doi.org/10.1126/science.1238411.

Pascual-Marqui, R.D., 2007. Instantaneous and Lagged Measurements of Linear and Nonlinear Dependence between Groups of Multivariate Time Series: Frequency Decomposition arXiv:0711.1455 [stat.ME].

Pascual-Marqui, R.D., 2002. Standardized low-resolution brain electromagnetic tomography (sLORETA): technical details. Methods Find. Exp. Clin. Pharmacol. 24 (D), 5–12.

Pascual-Marqui, R.D., Sekihara, K., Brandeis, D., Michel, C.M., 2009. Imaging the electric neuronal generators of EEG/MEG. In: Michel, C.M., Koenig, T., Brandeis, D., Gianotti, L.R.R., Wackermann, J. (Eds.), Electrical Neuroimaging. Cambridge University Press, pp. 49–78. https://doi.org/10.1017/CBO9780511596889.004.

Patel, A.D., 2007. Music, Language, and the Brain. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195123753.001.0001.

Patel, A.D., 2003. Language, music, syntax and the brain. Nat. Neurosci. 6, 674–681. https://doi.org/10.1038/nn1082.

Penny, W., Holmes, A., 2003. Random-effects analysis. In: Frackowiak, R.S.J., Friston, K.J., Frith, C.D., Dolan, R.J., Price, C.J., Ashburner, J., Penny, W.D., Zeki, S. (Eds.), Human Brain Function, second ed. Elsevier Inc., pp. 843–850. https://doi.org/10.1016/B978-012264841-0/50044-5

Pesonen, M., Björnberg, C.H., Hämäläinen, H., Krause, C.M., 2006. Brain oscillatory 1–30 Hz EEG ERD/ERS responses during the different stages of an auditory memory search task. Neurosci. Lett. 399, 45–50. https://doi.org/10.1016/J.NEULET.2006.01.053.

Plack, C.J., Oxenham, A.J., Fay, R.R., Popper, A.N. (Eds.), 2005. Pitch: Neural Coding and Perception. Springer.

Profita, J., Bidder, T.G., 1988. Perfect pitch. Am. J. Med. Genet. 29, 763–771. https://doi.org/10.1002/ajmg.1320290405.

Raichle, M.E., 2015. The brain's default mode network. Annu. Rev. Neurosci. 38, 433–447. https://doi.org/10.1146/annurev-neuro-071013-014030.

Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. U.S.A. 98, 676–682. https://doi.org/10.1073/pnas.98.2.676.

Ramyead, A., Kometer, M., Studerus, E., Koranyi, S., Ittig, S., Gschwandtner, U., Fuhr, P., Riecher-Rössler, A., 2015. Aberrant current source-density and lagged phase synchronization of neural oscillations as markers for emerging psychosis. Schizophr. Bull. 41, 919–929. https://doi.org/10.1093/schbul/sbu134.

Rubinov, M., Sporns, O., 2010. Complex network measures of brain connectivity: uses and interpretations. Neuroimage 52, 1059–1069. https://doi.org/10.1016/j.neuroimage.2009.10.003.

Ruiz, M.H., Koelsch, S., Bhattacharya, J., 2009. Decrease in early right alpha band phase synchronization and late gamma band oscillations in processing syntax in music. Hum. Brain Mapp. 30, 1207–1225. https://doi.org/10.1002/hbm.20584.

Sacks, O., 2010. The Mind's Eye. Knopf. New York/Toronto.

Sauseng, P., Klimesch, W., 2008. What does phase information of oscillatory brain activity tell us about cognitive processes? Neurosci. Biobehav. Rev. 32, 1001–1013. https://doi.org/10.1016/j.neubiorev.2008.03.014.

Schaefer, R.S., Vlek, R.J., Desain, P., 2011. Music perception and imagery in EEG: alpha band effects of task and stimulus. Int. J. Psychophysiol. 82, 254–259. https://doi.org/10.1016/j.ijpsycho.2011.09.007.

Schlaug, G., Jäncke, L., Huang, Y., Steinmetz, H., 1995. In vivo evidence of structural brain asymmetry in musicians. Science 267, 699–701. https://doi.org/10.1126/science.7839149.

Schoffelen, J.-M., Gross, J., 2009. Source connectivity analysis with MEG and EEG. Hum. Brain Mapp. 30, 1857–1865. https://doi.org/10.1002/hbm.20745.

Schölvinck, M.L., Leopold, D.A., Brookes, M.J., Khader, P.H., 2013. The contribution of electrophysiology to functional connectivity mapping. Neuroimage 80, 297–306. https://doi.org/10.1016/J.NEUROIMAGE.2013.04.010.

Schulze, K., Gaab, N., Schlaug, G., 2009. Perceiving pitch absolutely: comparing absolute and relative pitch possessors in a pitch memory task. BMC Neurosci. 10, 1–13. https://doi.org/10.1186/1471-2202-10-106.

Shulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J. Cogn. Neurosci. 9, 648–663. https://doi.org/10.1162/jocn.1997.9.5.648.

Silbert, L.J., Honey, C.J., Simony, E., Poeppel, D., Hasson, U., 2014. Coupled neural systems underlie the production and comprehension of naturalistic narrative speech. Proc. Natl. Acad. Sci. U.S.A. 111, E4687–E4696. https://doi.org/10.1073/pnas.1323812111.

Sporns, O., Chialvo, D.R., Kaiser, M., Hilgetag, C.C., 2004. Organization, development and function of complex brain networks. Trends Cogn. Sci. 8, 418–425. https://doi.org/10.1016/J.TICS.2004.07.008.

Szucs, D., Ioannidis, J.P.A., 2017. Empirical assessment of published effect sizes and power in the recent cognitive neuroscience and psychology literature. PLoS Biol. 15, e2000797 https://doi.org/10.1371/journal.pbio.2000797.

Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. Comput. Intell. Neurosci. 2011, 13. https://doi.org/10.1155/2011/879716.

Theusch, E., Basu, A., Gitschier, J., 2009. Genome-wide study of families with absolute pitch reveals linkage to 8q24.21 and locus heterogeneity. Am. J. Hum. Genet. 85, 112–119. https://doi.org/10.1016/j.ajhg.2009.06.010.

Theusch, E., Gitschier, J., 2011. Absolute pitch twin study and segregation analysis. Twin Res. Hum. Genet. 14, 173–178. https://doi.org/10.1375/twin.14.2.173.

van den Heuvel, M.P., de Lange, S.C., Zalesky, A., Seguin, C., Yeo, B.T.T., Schmidt, R., 2017. Proportional thresholding in resting-state fMRI functional connectivity networks and consequences for patient-control connectome studies: issues and recommendations. Neuroimage 152, 437–449. https://doi.org/10.1016/j.neuroimage.2017.02.005.

Van Wijk, B.C.M., Stam, C.J., Daffertshofer, A., 2010. Comparing brain networks of different size and connectivity density using graph theory. PLoS One 5. https://doi.org/10.1371/journal.pone.0013701.

Varela, F., Lachaux, J.-P., Rodriguez, E., Martinerie, J., 2001. The brainweb: phase synchronization and large-scale integration. Nat. Rev. Neurosci. 2, 229–239. https://doi.org/10.1038/35067550.

Wagner, M., Fuchs, M., Kastner, J., 2003. Evaluation of sLORETA in the presence of noise and multiple sources. Brain Topogr. 16, 277–280. https://doi.org/10.1023/B:BRAT.0000032865.58382.62.

Wayman, J.W., Frisina, R.D., Walton, J.P., Hantz, E.C., Crummer, G.C., 1992. Effects of musical training and absolute pitch ability on event-related activity in response to sine tones. J. Acoust. Soc. Am. 91, 3527–3531. https://doi.org/10.1121/1.402841.

Wendling, F., Ansari-Asl, K., Bartolomei, F., Senhadji, L., 2009. From EEG signals to brain connectivity: a model-based evaluation of interdependence measures. J. Neurosci. Methods 183, 9–18. https://doi.org/10.1016/J.JNEUMETH.2009.04.021.

Wengenroth, M., Blatow, M., Heinecke, A., Reinhardt, J., Stippich, C., Hofmann, E., Schneider, P., 2014. Increased volume and function of right auditory cortex as a marker for absolute pitch. Cerebr. Cortex 24, 1127–1137. https://doi.org/10.1093/cercor/bhs391.

Wu, C., Kirk, I.J., Hamm, J.P., Lim, V.K., 2008. The neural networks involved in pitch labeling of absolute pitch musicians. Neuroreport 19, 851–854. https://doi.org/10.1097/WNR.0b013e3282ff63b1.

Xia, M., Wang, J., He, Y., 2013. BrainNet Viewer: a network visualization tool for human brain connectomics. PLoS One 8, e68910. https://doi.org/10.1371/journal.pone.0068910.

Yordanova, J.Y., Kolev, V.N., Başar, E., 1998. EEG theta and frontal alpha oscillations during auditory processing change with aging. Electroencephalogr. Clin. Neurophysiology Evoked Potentials Sect. 108, 497–505. https://doi.org/10.1016/S0168-5597(98)00028-8.

Zalesky, A., Fornito, A., Bullmore, E.T., 2010. Network-based statistic: identifying differences in brain networks. Neuroimage 53, 1197–1207. https://doi.org/10.1016/j.neuroimage.2010.06.041.

Zamorano, A.M., Cifre, I., Montoya, P., Riquelme, I., Kleber, B., 2017. Insula-based networks in professional musicians: evidence for increased functional connectivity during resting state fMRI. Hum. Brain Mapp. 38, 4834–4849. https://doi.org/10.1002/hbm.23682.

Zatorre, R.J., 2005. Music, the food of neuroscience? Nature 434, 312–315. https://doi.org/10.1038/434312a.

Zatorre, R.J., 2003. Absolute pitch: a model for understanding the influence of genes and development on neural and cognitive function. Nat. Neurosci. 6, 692–695. https://doi.org/10.1038/nn1085.

Zatorre, R.J., Baum, S.R., 2012. Musical melody and speech intonation: singing a different tune. PLoS Biol. 10, e1001372 https://doi.org/10.1371/journal.pbio.1001372.

Zatorre, R.J., Belin, P., Penhune, V.B., 2002. Structure and function of auditory cortex: music and speech. Trends Cogn. Sci. 6, 37–46. https://doi.org/10.1016/S1364-6613(00)01816-7.

Zatorre, R.J., Chen, J.L., Penhune, V.B., 2007. When the brain plays music: auditory–motor interactions in music perception and production. Nat. Rev. Neurosci. 8, 547–558. https://doi.org/10.1038/nrn2152.

Zatorre, R.J., Perry, D.W., Beckett, C.A., Westbury, C.F., Evans, A.C., 1998. Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. Proc. Natl. Acad. Sci. U.S.A. 95, 3172–3177. https://doi.org/10.1073/pnas.95.6.3172.

Zuk, J., Benjamin, C., Kenyon, A., Gaab, N., 2014. Behavioral and neural correlates of executive functioning in musicians and non-musicians. PLoS One 9, e99868. https://doi.org/10.1371/journal.pone.0099868.